INHERITANCE OF SEX IN LYCHNIS[1]

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(WITH TWO FIGURES)

Since CORRENS (4) made his brilliant investigations with Bryonia, in which he showed that crosses between the monoecious *B. alba* and the two sexes of the dioecious *B. dioica* do not give equivalent results in regard to the sex of the offspring, and since DONCASTER and RAYNOR (6) published their equally interesting studies with the currant moth, *Abraxas grossulariata*, and its variety *lacticolor*, in which it was found that reciprocal crosses were not equal with respect to sex, but that the Mendelian color character of the variety *lacticolor* is sex-limited, the interest of all students of genetics has been more or less strongly directed toward the problems of sex inheritance, and toward the attempt to describe or explain the heredity of sex on the basis of Mendelian inheritance.

It has been of great interest to find that these two classic cases of Bryonia and Abraxas apparently lead to opposite conclusions as to which sex determines the sex of the offspring, but both seem to favor the conception that one sex is homozygous with respect to sex, and the other heterozygous. BATESON (1) attempts to make the results with Bryonia agree with those in Abraxas, but his interpretation is certainly not as simple as that of CORRENS. BATESON's explanation would require that *Bryonia alba* be gynodioecious, having larger numbers of pure females than of monoecists, instead of being wholly monoecious as described in the manuals. It does not seem likely that so striking a relation as this would have been overlooked by the taxonomists. Moreover, in the attempt to bring harmony between Bryonia and Abraxas, BATESON introduces fully as fundamental inharmony between the two species of Bryonia, when he assumes that the males of *B. dioica* are pure males with pollen bearing only the male character, while the pollen of *B. alba* is all female. Certainly we are justified in expecting a more complete

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harmony among the species of a single genus than between a species of plants and a species of animals. CASTLE (**3**) has also attempted to relate the Bryonia and Abraxas types of behavior by the assumption that in each case the female is the equivalent of the male plus an x element, the female in Bryonia being a *positive* homozygote and the male a heterozygote, while in Abraxas the female is a heterozygote and the male a *negative* homozygote. This explanation recognizes that Bryonia and Abraxas present fundamentally different conditions.

It is not my intention to present a general discussion of the present state of our knowledge regarding the inheritance of sex, as this has been well done recently by WILSON (**12**), CASTLE (**3**), BATESON (**1**), DONCASTER (**5**), and MORGAN (**8**). However, it may be said that the number of studies which have been made in this field are entirely too few as yet to warrant far-reaching generalizations on the question of sex inheritance, and further data bearing on the subject will be awaited with great interest. It has appeared to me that a serious criticism can be offered to the results of crosses between *Bryonia alba* and *B. dioica* as a basis for conclusions regarding the whole problem of sex inheritance. These crosses are interspecific, and, as is very often true of crosses between distinct species, the sterility of the F_1 offspring did not allow any test of the correctness of assumptions regarding the gametic composition of the hybrids. While it is true that in many species-crosses in which the hybrids are fertile, certain characteristics segregate normally, it has not been uncommon to find that many characters do not segregate, or at least that their segregation is very doubtful and obscure. The simple, typical segregation of characters is best exemplified by the most closely related forms, between which also the fertility is most perfect, and this may be expected to hold true of sex characters as well as of other alternative characters.

BATESON (**1**, p. 166) has repeated the experiments with Bryonia and has fully confirmed the results of CORRENS. BATESON is also convinced of the unsafe character of the Bryonia results as a basis for generalizations, and says that "the relation of dioecious to hermaphrodite and monoecious forms will not in all probability be satisfactorily or rapidly elucidated until some case can be found in which the two types can be crossed together with a fertile result."

I have some material now in hand which meets this requirement, but have not yet continued the experiments long enough to allow more than a preliminary report upon its behavior. For several years I have been investigating the sex ratios in *Lychnis dioica* L., and for this purpose have made carefully controlled pollinations yearly in this usually dioecious species. It was my good fortune during the summer of 1908 to find among these pure-bred cultures six hermaphrodite individuals, the first which I had seen in the several years during which I had been working with this species, in which time I had examined some 8000 pedigreed individuals. In the past season I have noted eight hermaphrodites, usually more or less imperfect, in pure-bred normal families including a total of 10,320 individuals. Only two of these eight were well developed and appeared to be fully functional both as males and females.

Although the occasional occurrence of hermaphrodite individuals in this species has been frequently noted,[2] I have never seen any of them growing wild in the vicinity of Cold Spring Harbor, where the original material for my cultures was collected. STRASBURGER (11) found that hermaphrodite plants in his cultures at Bonn were invariably affected by a smut, *Ustilago violacea*, which fruits in the anthers, and he ventured the suggestion that all the reported hermaphrodites in this species may have been such diseased individuals; but, fortunately for my experiments, *Ustilago violacea* has never appeared among my Lychnis cultures, and some, at least, of the hermaphrodite individuals were capable of functioning both as males and females. Five of the hermaphrodites found in 1908 were members of a single family (0739). Several of these hermaphrodite mutants did not have the ovaries and pistils fully developed, and consequently my ability to secure offspring from them was somewhat limited. However, during the past summer, I had 13 families in which one of these hermaphrodite plants entered as either the male or female parent. Two of the six original hermaphrodites died before I had opportunity to use them in crossing. Of the remaining four, two were successfully self fertilized, and one of these was also successfully used as a mother in crosses with a normal male.

[2] See PENZIG, O., Pflanzenteratologie 1:300; and KNUTH, P., Handbuch der Blütenbiologie 2[1]:174, 175.

For convenience, I will designate the four plants successfully used in breeding by the letters *A*, *B*, *C*, and *D*. When *A* was self fertilized it produced, as a result of two different operations, 33 females and 25 hermaphrodites. When its pollen was used to fertilize four different females, the resultant progenies consisted of 236 females, 161 hermaphrodites, and 2 males. When castrated and fertilized with pollen from a normal male, *A* gave rise to a progeny of 21 females, 2 hermaphrodites, and 11 males. *B* was also self fertilized and gave a progeny of 110 females and 95 hermaphrodites. When pollen of *B* was used to fertilize three different females, it produced 162 females and 144 hermaphrodites. It is thus seen that the two plants, *A* and *B*, showed identical behavior and together produced self fertilized offspring consisting of 143 females and 120 hermaphrodites, and when crossed with females gave a total of 398 females, 305 hermaphrodites, and 2 males. In any explanation of these results the occurrence of these two males will probably have to be left aside as wholly exceptional. Only further breeding will show whether they were true males, or hermaphrodites with pistils suppressed, perhaps, by some cause external to the germ cells. Plants *C* and *D* gave quite a different result. Attempts to self fertilize them and to cross them with normal males all proved futile, though more persistent efforts perhaps might have succeeded. Both were used as pollen parents in crosses with normal females. In such a cross *C* gave a progeny of 39 females and 55 normal males, and *D* gave 26 females and 18 normal males. The details of the several crosses are given in table I, p. 114.

Considering first plants *A* and *B*, and leaving out of consideration for the present the two males occurring in crosses between females and hermaphrodites, and the two hermaphrodites which appeared in the cross between a hermaphrodite and a normal male, it is apparent that the hermaphrodite character belongs only to the males, for in the families in which these hermaphrodites were the pollen parents, the offspring always showed the same ratios of females and hermaphrodites that would have been expected of females and males, had a normal male been used as the pollen parent.

It is clear that the hermaphrodite individuals, *C* and *D*, belong to an entirely different category from *A* and *B*, for in the families

produced by using them as pollen parents, the offspring are exactly the same as if normal males had been used. In *A* and *B* the hermaphrodite character is borne by the male germ cells and is fully hereditary. In *C* and *D* the hermaphrodite character may have been purely somatic, in no wise affecting the germ cells, and therefore incapable of hereditary transmission; or, in case the factor for hermaphroditism is independent of the sex-producing genes, *A*

TABLE I

Pedigree no.	Cross	Result
08115.........	☿×self (*A*)	24♀:19☿
08117.........	☿×self (*A*)	9♀:6☿
08119.........	☿×self (*B*)	110♀:95☿
Total	☿×self	143♀:120☿
0869..........	♀×☿ (*A*)	58♀:36☿ :1♂
08118.........	♀×☿ (*A*)	60♀:40☿ :1♂
08127.........	♀×☿ (*A*)	51♀:52☿
08149.........	♀×☿ (*A*)	67♀:33☿
08106.........	♀×☿ (*B*)	53♀:50☿
08128.........	♀×☿ (*B*)	50♀:51☿
08150.........	♀×☿ (*B*)	59♀:43☿
08125.........	♀×☿ (*C*)	39♀:0 :55♂
08132.........	♀×☿ (*D*)	26♀:0 :18♂
Total	♀×☿ { *A* and *B* *C* and *D*	398♀:305☿: 2♂ 65♀:0 :73♂
08116.........	☿ (*A*)×♂	21☿:2♀ :11♂

and *B* may have been homozygous and *C* and *D* heterozygous with respect to the hermaphrodite modifier.

That males, which are assumed to be heterozygous and to contain both the male and female tendencies, should occasionally show the development of characters of both the sexes as the result of some accident or environmental influence upon an individual, without in any way changing the character of the germ cells produced by that individual, is quite conceivable. The occurrence of these two different types of hermaphrodite individuals harmonizes well with many experiences met with in other studies in heredity, which have led JOHANNSEN (7) to distinguish between genotypes and phenotypes. These four hermaphrodite individuals, *A*, *B*, *C*, and *D*, belong to a single phenotype, but to two genotypes.

If now we compare these results in Lychnis with those of CORRENS in Bryonia, still leaving out of account the two exceptional males and the two hermaphrodites which occurred in pedigree no. 08116, we find that the difference is a consistent one. This comparison may be conveniently made in the following table:

TABLE II

Cross	Bryonia	Lychnis
♀×♂	♀ and ♂	♀ and ♂
☿×♂	♀ and ♂	♀ and ♂
♀×☿	♀	♀ and ☿
☿×☿	☿	♀ and ☿

In the first place, it is seen that all crosses between normal females and normal males in Lychnis result in females and normal males, just as in *Bryonia dioica*, and the same thing is true in both cases when the hermaphrodite is fertilized by a normal male. The result of self fertilizing the hermaphrodites of Lychnis, however, is (presumably) quite different from the result of self fertilizing *Bryonia alba*, for Lychnis gives rise to a progeny of females and hermaphrodites, while Bryonia (presumably) gives rise to only monoecists or hermaphrodite individuals. A similar difference is observable between these two classes of material when normal females are fertilized by pollen of hermaphrodites, as Bryonia produces in this case only females, while Lychnis produces females and hermaphrodites.

These results suggest that the differences between Bryonia and Lychnis are rather simple ones. The fact that the hermaphrodites take the place of males in each family whose male parent was a hermaphrodite, permits no other reasonable conclusion than that the hermaphrodite Lychnis is a modified male; and the capacity of the male to be thus modified so as to allow the development of both male and female organs, strongly favors the view that the male is heterozygous, as has been assumed by CORRENS (4) and CASTLE (3) for Bryonia, and as demonstrated by WILSON and his students for many insects.

There are now several possibilities regarding the nature of the females. CASTLE (2) long ago suggested that the female, as well as the male, is heterozygous, but in his latest communication on sex (CASTLE 3) he definitely abandons this view and holds that in all

cases only one sex is heterozygous and the other is homozygous; and this is the conception now generally entertained by those who adopt a Mendelian explanation of sex. According to this view, if the male is heterozygous, as has just been decided to be the case in Lychnis, the female must be homozygous. As there are two kinds of homozygotes, namely, "positive" and "negative" (SHULL 9), there remain two possibilities regarding the nature of the female; it may be either a positive homozygote or a negative homozygote. While either of these assumptions will explain about equally well the facts brought to light in Bryonia, neither will fit all those observed in Lychnis without encountering important difficulties.

Making first the supposition that the female is a positive homozygote, as suggested by CASTLE (3), all conditions found in Bryonia will be satisfied if it be also assumed that *B. alba* is a homozygous monoecist (a modified female condition in this case) in which the absence of the monoecious character is dominant over its presence. The sterility of the F_1 hybrids in Bryonia unfortunately makes it impossible to test the correctness of these assumptions. It is less easy to make a positive homozygous condition of the female fit the results found in Lychnis as described in this paper. This can be done, however, by assuming: (*a*) that all egg cells of both females and hermaphrodites carry the gene for the female sex, and not that for hermaphroditism; and (*b*) that all the sperms of the hermaphrodites carry a gene for the hermaphrodite modification, regardless whether they possess the gene for the female sex (the "*x* element") or not. The first of these assumptions seems necessary from the fact that the results are identical in each case, whether a female or a hermaphrodite is used as the female parent; and the second from the fact that females and hermaphrodites result from pollinating a normal female by pollen from a hermaphrodite. The second proposition might be replaced by one involving spurious allelomorphism. It is expected that a second generation will demonstrate the correctness or incorrectness of these several hypotheses.

The alternative assumption, namely, that the female is a negative homozygote, will just as simply represent the conditions of the F_1 generation. If the monoecious character in Bryonia be considered a modified male condition similar to the hermaphrodite character of

Lychnis, the difference between Bryonia and Lychnis is reduced to a question of dominance of the hermaphrodite (or modified male) condition. In order that *Bryonia alba* should breed true, the monoecious (or modified male) character must be homozygous. The fact that in Bryonia a cross between the female *B. dioica* and the monoecious *B. alba* produces only females, indicates that the monoecious character is capable of coming to full expression only when present in the homozygous state. In other words, while the monoecists are modified positive male homozygotes, absence of this modified male character is almost perfectly dominant over its presence, so that the heterozygous individuals which constitute the F_1 of this cross almost or quite completely lack the male character. In this connection the occurrence of occasional male flowers on a few of these females of the F_1 may be of interest as showing a slight influence of the unpaired gene for the modified male or monoecious sex.

In Lychnis, on the other hand, the presence of the hermaphrodite character is dominant over its absence, as demonstrated by the fact that the hermaphrodite mutants are heterozygous with respect to sex. In the following table a comparison may be made between the two methods of explaining the character of the F_1 hybrid generation:

TABLE III

ASSUMPTION: The female is a positive homozygote

CROSS	BRYONIA			LYCHNIS		
	Assumed character of parental gametes	Resultant composition of offspring	Somatic type of offspring	Assumed character of parental gametes	Resultant composition of offspring	Somatic type of offspring
♀×♂	♀♀×♀	♀♀ and ♀	♀ and ♂	♀♀×♀	♀♀ and ♀	♀ and ♂
☿×♂	☿☿×♀	☿♀ and ☿	♀ and ♂	♀♀×♀	♀♀ and ♀	♀ and ♂
♀×☿	♀♀×☿☿	♀☿	♀	♀♀×☿ˇ	♀☿ and ☿	♀ and ☿
☿×☿	☿☿×☿☿	☿☿	☿	♀♀×☿ˇ	♀☿ and ☿	♀ and ☿
ASSUMPTION: The female is a negative homozygote						
♀×♂	♀♀ ×♀♀♂	♀♀ and ♀♀♂	♀ and ♂	♀♀×♀♀♂	♀♀ and ♀♀♂	♀ and ♂
☿×♂	♀♀☿☿×♀♀♂	♀♀☿ and ♀♀☿♂	♀ and ♂	♀♀×♀♀♂	♀♀ and ♀♀♂	♀ and ♂
♀×☿	♀♀ ×♀♀☿☿	♀♀☿	♀	♀♀×♀♀☿	♀♀ and ♀♀☿	♀ and ☿
☿×☿	♀♀☿☿×♀♀☿☿	♀♀☿☿	☿	♀♀×♀♀☿	♀♀ and ♀♀☿	♀ and ☿

No decision can be made between the two methods of explanation contrasted in this table until the F_2 has shown the dependence or

independence of the gene whose presence results in the hermaphrodite modification of the male. If the females may carry the hermaphrodite modification as a latent character, and if the hermaphrodites of the F_1 differ in their gametic composition from those of the P_1 generation, the hypothesis that the female is a positive homozygote may be substantiated; but if the hermaphrodites of the F_1 are identical in their behavior with those of the P_1, and if the hermaphrodite modification cannot be transmitted through the female, the results will support the hypothesis that the female is a negative homozygote.

It is not at all improbable that the hermaphrodites discussed above as *C* and *D* differed from *A* and *B* in having the gene for the hermaphrodite modification in the heterozygous state, while *A* and *B* were homozygous with respect to this gene. If this should be correct, then *C* and *D* were of the type which will appear in the F_1 of crosses between normal females and such hermaphrodites as *A* and *B*, in case the hermaphrodite modification is independent of the male germ cells. The occurrence of such hermaphrodites as *C* and *D* may be accepted as rather favorable to the view that the female is a positive homozygote.

There is one fundamental difficulty with any hypothesis which assumes that the hermaphrodites are heterozygous. The eggs of these hermaphrodites are of a single kind with respect to sex, all carrying the female character. This difficulty is inherent in the material itself, however, and is not opposed in any way to the assumption that the normal females are either positive or negative homozygotes, for the male germ cells of the hermaphrodites are clearly of two types as required by the hypothesis that these hermaphrodite plants are heterozygous. Cytological investigations of oogenesis in the hermaphrodites may perhaps give a complete solution to the exceptional situation presented by the egg cells. If the females are positive homozygotes there may be simply a failure of those eggs to develop which do not possess the gene for the female sex. If the female is a negative homozygote, there may be a failure of those eggs which possess the male gene, or there may be an exclusion of this gene during oogenesis.

While I have left out of account the two hermaphrodite individuals in the cross (08116) between a hermaphrodite and a normal male,

I am not unmindful of their possible importance. The number of offspring of this combination was too small to enable one to be sure that these are not mutants which bear no necessary relation to the fact that their mother was a hermaphrodite. It was found particularly difficult to secure offspring of crosses of this type, as the flowers were very often caused to drop off as a result of the process of castration. Very often also in the flowers of hermaphrodite plants the pistils are immature at the time the anthers are ready to open, and after castration these pistils frequently develop no farther, in which case there is no possibility of effecting fertilization. The occurrence of these two hermaphrodite plants in no. 08116 offers a further suggestion that the hermaphrodite character may be capable of independent movement, and that consequently it may be carried in some manner or to some degree by the female. This suggestion especially commends itself from the fact that the occurrence of the male and female organs on the same plant, as CORRENS (4) has pointed out, constitutes in effect a mosaic, and it is well known that mosaic inheritance is often dependent upon the presence of a definite separate unit for the mosaic condition. If further investigation should demonstrate that the hermaphrodite character may be transmitted through the female, as is suggested by this one family, we will be forced to the conclusion that here also the existence of a unit for the mosaic condition is present. In whatever manner the male may be converted into a hermaphrodite, the results seem to demonstrate that in Lychnis, as in Bryonia, *it is the male which is heterozygous* and which carries both male- and female-producing genes as concluded by CORRENS, and not the female as assumed by BATESON.

The demonstration that the hermaphrodite of *Lychnis dioica* is a modified male indicates that STRASBURGER (11) was mistaken in his interpretation of the effects produced by *Ustilago violacea* upon this species. He believed that the infected plants were females in which the development of stamens was stimulated by the attack of the fungus. Instead of this it is probable that they were males in which the disease somewhat lessened or modified the dominance of the male character, thus allowing the female organs to develop; or, if the female is a positive homozygote, the disease may be assumed to have stimulated the single female gene or x element of the male

to develop the female organs as well as the male organs. STRASBURGER states that the development of the stamens in the diseased plants was correlated with an elongation of the floral axis between the calyx and corolla (a character peculiar to flowers of the male plants), and that not infrequently the infected plants gave the impression that they were males. On the other hand, the fibrovas-

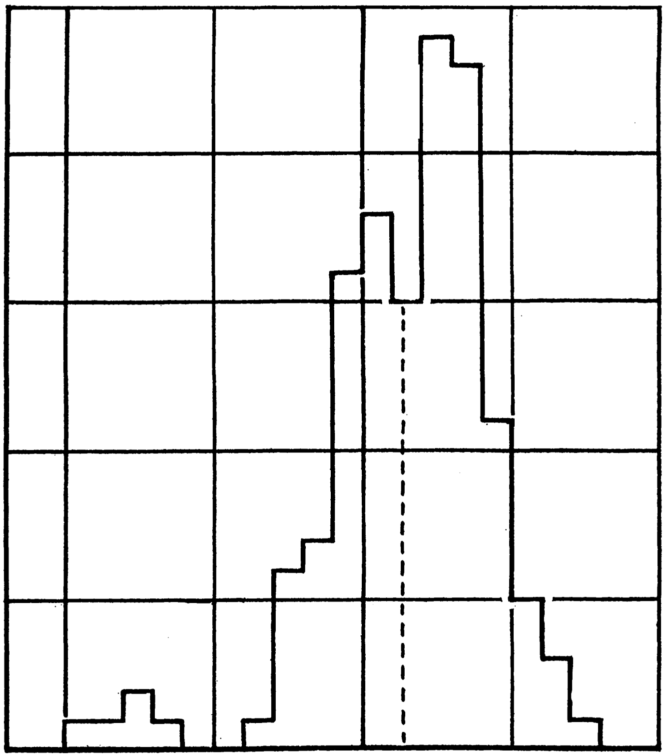

FIG. 1.—Variation in percentages of females in 135 families of *Lychnis dioica*.

cular system of the calyx in infected plants more nearly assumed the distinctive features of the normal female flowers. The appearance of this secondary female character may be as readily accounted for as the appearance of the female sex organs themselves, on the ground of modified dominance of the male or of the female character in a heterozygous male.

CORRENS has pointed out that the determination of sex ratios is quite a different matter from the determination of sex, and we must

maintain that this is so, provided sex is inherited as a Mendelian character. But if sex inheritance be not primarily Mendelian, but only associated with and perhaps determined by Mendelian charac-

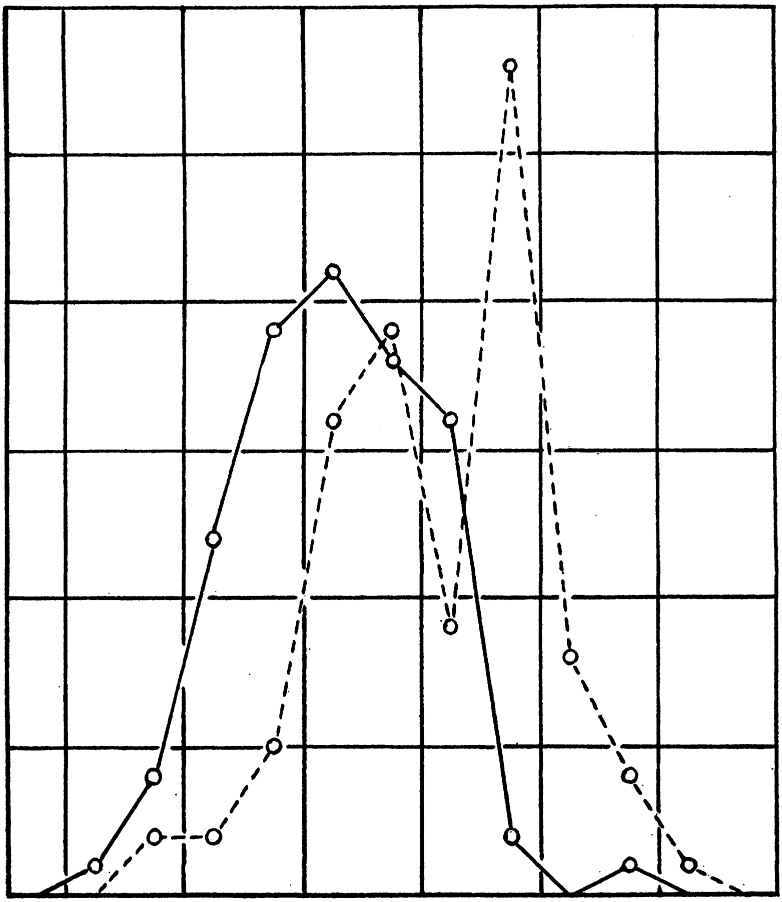

FIG. 2.—Variation in percentages of females and in percentages of purple-flowered plants in 94 families of *Lychnis dioica* produced by crossing heterozygous purple with white; broken curve represents females; both curves if monomodal belong to PEARSON'S Type I. See constants in table IV.

ters in a few cases, the determination of a sex ratio might not be a process distinct from the inheritance of sex itself.

The assumption that the sexes differ from each other by a single unit character, and that one sex is heterozygous and the other homo-

zygous with respect to this character, would demand equality in the average numbers of the two sexes; but each year *Lychnis dioica* has produced on the average a considerable excess of females, while the ratios in different families range all the way from less than 5 per cent. female to nearly 90 per cent. female. The percentages of females in 135 families reared during the summer of 1909 are shown in the form of a variation curve in *fig. 1*. It is difficult to believe that a family of 4 females and 100 males or of 87 females and 10 males is theoretically referable to a ratio of 1:1. In 1909 my cultures of *Lychnis dioica*, taken collectively, consisted of 6366 females and 4831 males (including hermaphrodites), or a ratio of 1.32:1, which agrees very well with ratios between 1.20:1 and 1.40:1 reported by STRASBURGER (**11**). After carrying on extensive experiments on the influence of various environmental factors, with negative results, STRASBURGER reached the conclusion that the sex ratio is determined by inherent factors. This is only another way of saying that it is hereditary in some sense. I have been attempting for several years to test the heredity of the sex ratios, but have not yet found the key to the situation. It is hoped that the numerous crosses which have been made will in the near future throw some light upon the significance of these exceedingly variable ratios and allow the causes which determine them to be understood.

In order to compare the variation in these sex ratios with that in a character known to be Mendelian, I have plotted curves representing the percentage of females and the percentage of purple-flowered individuals in all families (94 in number) raised during the years 1907, 1908, and 1909, which were produced by the union of heterozygous purple with white (see *fig. 2*). The variation constants of the two curves appear in the following table:

TABLE IV

VARIATION CONSTANTS OF CURVES CONTRASTED IN *fig. 2*

	Percentage females	Percentage purples
Mean	61.223 ±0.630	52.606 ±0.551
Standard deviation	9.051 ±0.445	7.925 ±0.490
Coefficient of variability	14.784 ±0.742	15.064 ±0.758
Theoretical mode	62.933 ±0.686	52.353 ±0.600
Coefficient of skewness	−0.0990±0.0062	+0.0282±0.0062

Aside from the remarkable difference in the value of the means, the two curves are skewed in opposite directions, the strong negative skewness and suggested bimodality of the sex curve, as contrasted with the nearly normal character of the curve for color, being particularly noteworthy. The variability represented by these two curves is properly compared by means of the standard deviations, and not by the coefficient of variability, since we are dealing here with groups of variates having similar theoretical limits of range, and similar expected mean values. On this basis the sex ratios show considerably greater variability than those of the color character. This is especially interesting in view of the fact, pointed out elsewhere (SHULL **10**), that crosses between heterozygous purple and white *Lychnis dioica* may frequently result in other ratios than 1:1, owing to the part taken by several distinct genes in the production of the purple colors in this species, and that therefore the data for the color curve may be somewhat heterogeneous, while the sex data are at present assumed to be homogeneous.

Summary

Hermaphrodite mutants occur in pure-bred families of *Lychnis dioica* L., the ratio of mutability being somewhat less than 1:1000.

None of these hermaphrodites was diseased and several were fully functional both as females and males, thus negativing the suggestion of STRASBURGER that the hermaphrodites in this species may always be due to the attacks of the smut, *Ustilago violacea.*

In their hereditary relations these hermaphrodites were of two kinds, some behaving like normal males, others having the capacity of transmitting the hermaphrodite character to their male offspring. This second class of hermaphrodites when self fertilized, or crossed with normal females, gives progenies consisting of normal females and hermaphrodites, and when fertilized by normal males gives normal females and normal males.

The hermaphrodite individuals are modified males, for in all families in which these hermaphrodites were the pollen parents the offspring showed the same ratios of females and hermaphrodites as would have been expected of females and males had a normal male been used as the pollen parent.

These results agree in a general way with those of Bryonia in that they demonstrate the homozygous character of the females and the heterozygous character of the males in Lychnis.

Whether the females are positive or negative homozygotes cannot be determined from the F_1, as both assumptions can be made to fit the facts by the aid of simple correlative hypotheses whose correctness or incorrectness can be determined only by further breeding.

A fundamental difficulty in either case is found in the fact that the egg cells of the hermaphrodites are apparently of a single type, all possessing the female-producing gene. The assumption that the hermaphrodites are heterozygous leads us to expect equal numbers of two different types of egg cells. Cytological studies may perhaps explain this difficulty. The male germ cells of the same plants are of two types, as required by theory.

The occurrence of two hermaphrodite individuals in a progeny produced by a cross between hermaphrodite and normal male suggests the possibility that the hermaphrodite character may also be transmitted through the female. This fact, together with the occurrence of two genotypes among the hermaphrodites, is held to be slightly favorable to the view that the female is a positive homozygote.

The demonstration that the hermaphrodite individuals of Lychnis are modified males indicates that STRASBURGER was mistaken in assuming that his hermaphrodites were diseased females. They were probably diseased males in which the dominance of the male character was modified by the fungus.

The sex ratios in Lychnis do not accord well with a theory of sex which requires males and females to be present in equal numbers. The ratios found in my cultures are in accord with those found by STRASBURGER, the average for the past year being 1.32 females to 1 male, with a very wide difference in the ratios of different families. The significance of these ratios is not yet understood.

When the variability in the sex ratios is compared with that in ratios produced by crossing heterozygous purple with white-flowered individuals, it is found that not only is there an undue departure in the sex ratios from the expected ratio 1 : 1, but also that there is greater variability in the sex ratios than in the color ratios, and that the curve is strongly negatively skewed and possibly not monomodal; while the

color curve derived from the same families is nearly normal; with the mean departing but little from the 50 per cent. required by Mendelian theory.

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